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XIII. "Contributions to the Anatomy of Fishes. II. The Air-Bladder and Weberian Ossicles in the Siluroid Fishes." By T. W. BRIDGE, M.A., Professor of Zoology in the Mason College, Birmingham, and A. C. HADDON, M.A., Professor of Zoology in the Royal College of Science, Dublin. Communicated by Professor NEWTON, F.R.S. Received June 9, 1892.

(Abstract.)

An abstract of the first part of this memoir, which dealt with the structure and relations of the air-bladder and Weber's ossicles in the Siluridæ, was published in the Proceedings of this Society three years ago ('Roy. Soc. Proc.,' vol. 46, 1889, pp. 309—328). The present contribution is a discussion of the physiology not only of this remarkable mechanism, but of the air-bladder in general.

There is a strong *a priori* probability that the Weberian mechanism is physiologically related to one of the several functions that have been ascribed to the auditory organ or to the air-bladder, but to which of them is a question by no means easy to answer. A preliminary difficulty to be encountered is the complex physiological character of the two organs, and, apart from our imperfect knowledge of the physiology of the several functions assigned to each, and especially in the case of the auditory organ of Fishes, a further difficulty is

afforded by the almost total absence of any experimental evidence directly bearing on the physiological significance of the Weberian ossicles; and while we desire to emphasise the danger of deducing function from facts of a purely anatomical nature, no other course has yet been adopted by previous writers on this subject, and at present is the only one open to us; consequently, any conclusions based upon data so frequently unreliable and misleading must partake rather of the nature of suggestions, and be accepted with considerable reserve. With the qualifications rendered necessary by these considerations, some light may possibly be thrown on this difficult problem by a careful inquiry as to how far the Weberian ossicles and the coadapted parts of the air-bladder and auditory organ are anatomically fitted to act as subsidiary or accessory structures in connection with any of the several functions assigned either to the air-bladder or auditory organ, while unsuited for association with others. By this means it may at least be possible to eliminate certain functions from any further consideration, and thereby considerably narrow the scope of future inquiry.

With this object we propose to discuss (I) how far the function of the Weberian mechanism is conditioned by the anatomical structure of the air-bladder and auditory organ, as well as by the character of the mechanism itself; (II) to which of the known functions of the air-bladder and auditory organ the Weberian ossicles are to be regarded as accessory structures; and (III) the utility of the mechanism to the Fish possessing it.

I. In all the Siluridæ normales the air-bladder may be regarded as consisting of two intercommunicating but physiologically distinct portions—a posterior, represented by the two lateral compartments, which is indistensible and inelastic, and always of greater internal capacity, and an anterior, which is always more or less elastic and expansible, but of less internal capacity than the former. The distensibility of the anterior chamber is, however, by no means uniform in all directions; on the contrary, the peculiar construction of the chamber and its intimate relations and connections with neighbouring skeletal structures render it absolutely inexpansible except laterally, that is, in a direction at right angles to its antero-posterior axis; and from the mode in which the fibres forming the lateral walls of the chamber converge in the dorsal wall, and become inserted into the crescentic processes of the tripodes, it becomes still more obvious that it is only by inward or outward bulgings of the lateral walls that variations in the internal condition of the air-bladder are able to set the Weberian ossicles in motion. It is scarcely necessary to point out that by this restriction of the expansion or contraction of the anterior chamber to movements of its lateral walls, the Weberian ossicles are rendered more suscep-

tible, and therefore capable of responding to smaller variations of internal gaseous tension by whatever cause produced than if the anterior chamber were equally elastic and expansible in all directions.

The increased delicacy of the Weberian mechanism in the Siluridæ normales, as compared with other Ostariophyseæ, is probably the cause of the extensive anchylosis of the anterior vertebræ, and their rigid articulation with the skull, for if flexibly articulated with one another and to the skull, so as to be able to participate in the lateral flexion of the vertebral column in ordinary locomotion, while at the same time the vertebræ and their processes retained their intimate relations with the air-bladder, the anterior chamber and Weberian ossicles could hardly fail to be affected by muscular compression. Hence, anchylosis of the anterior vertebræ becomes almost a necessity in the Siluridæ, if the Weberian mechanism is to remain unaffected by the more or less violent shocks produced by muscular contraction and relaxation. From a physiological point of view, it may be noted in connection with the Weberian ossicles, (*a*) that the anterior and crescentic processes of the tripodes are of approximately equal length, and hence the force and amplitude of all movements imparted to one extremity will be exactly reproduced, without augmentation, at the other; (*b*) the interposition of a lax, or at all events compressible, ligament (interossicular ligament) in the series of ossicles; and (*c*) the rudimentary and functionless condition of the intercalarium.

These and other facts suggest the conclusion that the Weberian apparatus is far better adapted to register the more forcible, even if more gradual, distensions or contractions of the anterior chamber, rather than slight or rapidly recurring vibrations of its lateral walls.

Finally, it may be affirmed that no differential action of the two auditory organs can possibly take place, at all events so far as impulses received through the Weberian mechanism are concerned, since the only channel through which any movement initiated in the fluids of the atrial cavities by the motion of the Weberian ossicles can reach them is the median, unpaired sinus endolymphaticus (the "sinus impar" of Weber); hence it must follow that each auditory organ will be affected by any such disturbances to an equal extent and at the same moment.

II. So far as the auditory organ is concerned, the functions of audition and equilibration or orientation have to be considered, and for the air-bladder those of phonation or sound production, respiration, accessory to audition, or its function may be purely hydrostatic.

Certain of these possible functions may be at once eliminated from any discussion as to the use of the Weberian mechanism. Equilibration may be dismissed, inasmuch as there can be no differential action of the two auditory organs. The absence of intrinsic muscular fibres

in the walls of the air-bladder, of extrinsic muscles in all but a few genera (Pimelodinæ), and of internal vibratory diaphragms, or other obviously vocal structures, is sufficient to prove that the air-bladder takes little or no part in this function, at all events by any of the ordinary methods known in other Fishes. The feeble vascularity of the air-bladder and the absence of any inspiratory or expiratory mechanisms are serious objections to its use as an ordinary respiratory organ.

In many Fishes the bladder appears to have a secondary relation to respiration by acting as a reservoir for the superabundance of oxygen introduced into the blood by the gills, which can be reabsorbed when required, but Moreau's experiments prove that those Fishes provided with a Weberian mechanism have a far less capacity for absorbing oxygen from the air-bladder than other Teleostei have under precisely similar conditions, and, further, that the capacity for oxygen absorption is always associated with the presence of retia mirabilia or vaso-ganglia, which, as our investigations prove, are invariably absent in all Siluridæ.

Very little is known about the physiology of hearing in Fishes, but we are unable to see that there is any need to assume that the conditions of subaqueous audition are very different to those in air, except in so far as the physical differences in the conductivity of the respective media are concerned. Sound vibrations travel much more rapidly in water than in air and to far greater distances, but they pass with difficulty from water to air, and conversely. Those sound vibrations which are too feeble to produce any appreciable effect on the external surface of the skull when they pass through air can, nevertheless, strongly impress the ear when propagated in water and the head of the observer is completely submerged (Colladon and Sturm). Sound waves impinging on the surface of a Fish's skull would therefore be readily conveyed to the perilymph and endolymph of the ear, and such sounds will, in all probability, be heard with greater rapidity and from greater distances than could possibly be the case under similar conditions in air.

The strongest objections to the auditory function of the air-bladder and Weberian mechanism (Weber's theory) are to be found in the imperfections of the apparatus. If vibrations can pass at all from the external medium to the gases contained within the air-bladder the transmission must be accompanied by a considerable loss of intensity, and this must especially be the case in those Ostariophyseæ in which the air-bladder is widely separated from the superficial skin by the liver and other organs and tissues. In many Siluridæ the walls of the air-bladder are too thick to admit of their vibrating synchronously with rapidly recurring sound waves. The inertia of the ossicles themselves, and the interposition between them of a compressible ligament,

are insuperable objections to this theory; and, moreover, the Fish could have no appreciation of the direction of the sounds conveyed through this mechanism. Finally, it may be affirmed that, contrary to what might be expected if so complicated a structure as the Weberian mechanism is an accessory to audition, there is absolutely no evidence of the existence of exceptional powers of hearing in the Siluridæ or any other Ostariophyseæ. For these reasons we conclude that the Weberian ossicles are in no way related to the function of hearing, even to the subordinate and qualified extent tacitly suggested by Hasse and Ramsay Wright.

The only remaining view is that the ossicles under consideration are accessory to the hydrostatic function of the air-bladder. Moreau, and later, Charbonnel-Salle, have completely refuted the older theory of this function, which has usually been associated with the name of Borelli. Summarising the conclusions which the experimental researches of these authors and certain other facts appear to warrant, it may be affirmed for Fishes in general:—

(*a.*) The function of the air-bladder is to render the Fish, bulk for bulk, of the same weight as the medium in which it lives. In this mean condition, or plane of least effort, the Fish acquires a capacity for the maximum amount of locomotion with a minimum of muscular effort.

(*b.*) In its movements of ascent or descent the Fish becomes exposed to augmented or diminished pressure, which, in each case, varies in amount according to the variable height of the superimposed column of water, and this leads to an expansion or contraction of the air in the air-bladder, and consequently to an increase or diminution in the volume of the Fish itself, and thereby to a corresponding alteration in its specific gravity, which may temporarily remove the animal from its normal plane of least effort.

(*c.*) The Fish has no power of varying the capacity of its air-bladder by direct muscular contraction, and its readjustment to a new plane of least effort results from a gradual increase or decrease in the amount and volume of the air contained within the air-bladder to an extent proportional to the new pressure and due to a corresponding modification of the processes concerned in the secretion or absorption of the contained gases. Hence, by this apparently automatic method of adjustment, the Fish will find, sooner or later, and whatever may be the depth of the water and the amount of external hydrostatic or atmospheric pressure, a plane of least effort, where it will again possess exactly the density of the water.

(*d.*) That Johannes Müller's theory of the displacement of the centre of gravity upon a longitudinal axis in the case of Fishes with a two-chambered air-bladder has no foundation in fact.

(*e.*) That, despite the obvious advantages which an air-bladder con-

fers upon its possessor, there are certain attendant disadvantages, of which, perhaps, the most important is the restriction of freedom of locomotion in a vertical direction, the result of the slowness with which the necessary secretion or absorption of gas takes place.

The conclusions embodied in the preceding sections relate more particularly to the Physoclisti, by far the largest group of Teleostean Fishes, but it may be pointed out that in a general way they apply also to the Physostomi, with, however, the qualification that in the great majority of the latter group the mechanical liberation of gas through the ductus pneumaticus takes the place of absorption as a means of adjustment to reduced hydrostatic pressures.

From the conclusions established by Moreau and Charbonnel-Salle it is obvious that the varying pressures to which the gases contained in the air-bladder are exposed constitute an important factor in the physiology of locomotion in Fishes, and hence, in the absence of any other tenable hypothesis as to its function, there is a strong antecedent probability in favour of the view which Hasse was the first to suggest, viz.:—that the object of the Weberian mechanism is to bring directly to the consciousness of the Fish the varying tensions of the gaseous contents of the air-bladder, due to the incidence of varying hydrostatic pressures. The late Dr. Sagemehl also adopted Hasse's view, at least, so far as to regard the mechanism as a register of pressure variations, but with this important modification, that it is not hydrostatic but atmospheric pressure which the Fish is thereby enabled to appreciate. There are, however, certain grave objections to Sagemehl's ingenious theory.

To a Fish at a depth of, say, six feet below the surface of the water, a variation of atmospheric pressure sufficient to raise or depress a column of mercury in a barometer to the extent of half an inch will only involve a variation of pressure amounting to less than one-tenth of the already existing hydrostatic pressure; and even this trifling difference will become relatively smaller as the depth at which the Fish lives becomes greater, while the ascent or descent of the Fish in the water to the extent of only seven inches would certainly mask any variation of atmospheric pressure to the extent indicated, seeing that the animal can have no power of differentiating the effects due to the incidence of the two pressures. A barometrical variation of even half an inch takes place but slowly, and rarely occurs in less time than several hours, and consequently could only be appreciated as distinct from hydrostatic pressure if the Fish remained at exactly the same depth in the water during the whole time that the barometrical variation was in progress. The maximum range of variation in atmospheric pressure, as measured by the barometer, is about two inches, but such variations occur only at considerable intervals of time, and then may take hours to accomplish. Even in this extreme case the

atmospheric pressure variation might be negatived by a variation of level in the water to extent of twenty-seven inches, or more or less completely masked by similar movements of still less extent during ordinary locomotion, or by the rise or fall of the tide in the case of the few estuarine or marine species. It may also be urged in opposition to the theory that there is no evidence that the Siluridæ, or any other Ostariophyseæ, are in any way different from other Fishes in being specially susceptible to atmospheric pressure variations, or that they possess any special capacity for anticipating impending changes in the weather. Sagemehl's theory being untenable, Hasse's view only remains. The general structure of the air-bladder, the mode of interconnection of the different Weberian ossicles, and their relations to the air-bladder and auditory organ, as well as the relations *inter se* of the two last-mentioned structures, are perfectly consistent with this theory, against which no anatomical objections can be urged, and equally inconsistent with any other at present suggested.

III. That the Weberian mechanism is of great functional importance to the Fish possessing it admits of no doubt. It is extremely improbable that so complicated and highly specialised a mechanism would have been evolved did it not confer some exceptional advantage upon its possessor, and that this is the case seems to be clearly demonstrated by the significant fact that the presence of the mechanism is characteristic of nearly all the dominant families of fresh-water Teleostei. The precise utility of the mechanism is, nevertheless, a very difficult problem. Assuming the correctness of Hasse's theory, it is inconceivable that the pressure variations, which it is the function of the Weberian apparatus to register, can arise from any other cause than the ascent or descent of the Fish in the water during ordinary locomotion, and this at once suggests that the advantage of the mechanism is directly related to some form of pressure adjustment. In dealing with this aspect of the question it becomes necessary to first consider the methods of pressure adjustment in Fishes in general.

Gaseous secretion and absorption are highly important factors in the adjustment of the volume of the gases contained in the air-bladder to variations of hydrostatic pressure. The conditions under which these processes take place have been experimentally investigated by Moreau, who has demonstrated that when the air is exhausted from the air-bladder (by means of an air-pump in the case of Physostomous Fishes, or by puncture in the Physoclisti) it takes from several hours to several days to restore the abstracted air by secretion and for the Fish to regain its normal liberty of movement. The rate of absorption is in fairly close agreement with that of secretion. It is obvious that the rapidity with which these processes take place is an important factor in determining how far they are likely to be available as

a means of pressure adjustment during ordinary locomotion, but unfortunately, in Moreau's experiments, the amount of gas previously abstracted from the air-bladder, or the extent of the pressure variation to which the organ was exposed, was often so considerable that from several hours to several days were required to restore the normal equilibrium of the Fish. No attempt has yet been made to obtain accurate measurements of the precise rate of secretion or absorption under conditions involving relatively small variations of level and pressure. Three important factors appear, however, to be well established :—(1) that gaseous secretion and absorption are relatively slow processes in all Fishes; (2) that, although retia mirabilia are not indispensable to these processes, there can be no doubt that both take place much more rapidly in Fishes that possess such structures than in those in which they are wanting; and (3) that increased hydrostatic pressure accelerates the rate of secretion, while diminished pressure exerts a similar influence on absorption.

In the case of the Physoclisti, which very generally possess retia mirabilia, but no pneumatic duct, gaseous secretion and absorption must be the only means of pressure adjustment; but how far these methods can be employed during the more or less rapid changes of level that occur in ordinary locomotion is doubtful, and, bearing in mind the relatively slow rate at which these processes take place, even in Fishes with retia mirabilia, we incline to the opinion that they are more likely to be of advantage to the Fish during such gradual changes of level as may occur in the course of diurnal, seasonal, or other periodic migrations than in ordinary locomotion. That this is the case seems to be suggested by many features in their habits, which tend to prove that most Physoclisti have but a comparatively restricted vertical range in so far as normal locomotion is concerned.

The relatively few Physostomi which possess an air-bladder and no ductus pneumaticus are in precisely the same position, as regards their mode of pressure adjustment, as the majority of the Physoclisti; and of the remainder, we may consider, in the first place, the Ostariophyseæ, which possess not only an open pneumatic duct and a Weberian mechanism but are without retia mirabilia.

The absence of retia mirabilia in all hitherto investigated Ostariophyseæ suggests that as a means of pressure adjustment gaseous secretion and absorption are of minor importance. On the other hand, Moreau's experiments prove that those Ostariophyseæ with which he experimented possess a great advantage over the Physoclisti in that they can, during ascent, more rapidly adjust the volume of gas in the air-bladder to decreased hydrostatic pressure by mechanically liberating a certain quantity of gas through the pneumatic duct than by relying solely on the absorptive capacity of the

walls of the air-bladder. Conversely, the typical Physoclisti have the advantage during descent. Moreau points out that a Fish incurs more danger by rising above the plane of least effort than by sinking below it. It is conceivable that a Physoclist, in the course of rapid ascent, might so far depart from its normal plane of equilibrium as to be forcibly carried to the surface of the water, and in that helpless condition fall an easy and conspicuous prey to predaceous Birds or Fishes. No special danger or inconvenience would result from a sudden and rapid descent, and it is at least possible that the increased secretion of gas which augmented pressure certainly conditions in the Physoclisti may not be altogether without effect in bringing about a more speedy re-adjustment to the greater pressure of a deeper level, even in the Ostariophyseæ, in spite of the absence of retia mirabilia. From these considerations it follows that, as compared with the Physoclisti, the Ostariophyseæ possess a far greater capacity for adapting themselves to rapid and extensive changes of level, more particularly in the direction of ascent; and many well-known facts in connexion with their habits support this conclusion.

The physiological relation of the Weberian ossicles to the hydrostatic function of the air-bladder is a problem which can only be satisfactorily solved by experimental inquiry. The evidence seems conclusive against assigning more than a very subordinate part to this mechanism, if any, in the way of controlling the absorption or secretion of gas; but it may, nevertheless, control or regulate the escape of gas through the ductus pneumaticus. A gradual distension of the air-bladder would be accurately measured by the recording lever (Weberian ossicles) and the increasing intensity of the stimulus imparted to the sensory epithelium of the auditory organ and to the saccular branches of the auditory nerve. The consequent reflex or voluntary efferent impulses may find expression in the exercise of some form of regulatory control over the liberation of gas through the pneumatic duct, so that only so much gas will be eliminated from time to time as may suffice to enable the Fish to retain its plane of equilibrium at all levels during ascent, notwithstanding the reduction of external hydrostatic pressure. Unfortunately there is but little anatomical and absolutely no experimental evidence as to how, or in what way, the escape of gas is regulated in accordance with these suggestions. Valvular structures have been found in the ductus pneumaticus in some Ostariophyseæ (*e.g.*, Cyprinidæ), and we have found unstriped muscle cells in its walls. It is probable, as suggested by Ramsay Wright, that the duct is not to be regarded as a mere channel for the escape of gas from the air-bladder, but rather as a structure which, under reflex control, actively participates in the process, possibly by peristaltic contractions. The air-bladder and pneumatic

duct exhibit some structural analogies to the gall-bladder and cystic duct of Mammalia, and bearing in mind that the absence of intrinsic muscles in the walls of the bladder is associated with the fact that the tension of the contained gases under the influence of reduced hydrostatic pressure will supply the needful expulsive force, it is by no means improbable that a close physiological parallelism may also exist with regard to the escape of their respective contents.

Whatever may be the precise nature of the controlling mechanism, the advantage to the Fish of some method of carefully graduated adjustment to pressure variations is sufficiently obvious. Without any form of regulatory control, and with an open ductus pneumaticus in free communication with the exterior, it may be surmised that the escape of gas would be continuous and unchecked, and might even involve a more or less complete exhaustion of the gas in the bladder as the pressure diminished, with the contingent disadvantage that the normal equilibrium of the Fish in the water would be greatly disturbed, and a considerable demand be made on the secretive activity of the bladder for the subsequent restoration of the gas. On the other hand, the existence of a controlling mechanism would ensure that only so much gas will be evolved as may suffice to maintain the Fish in a plane of equilibrium, and, at the same time, secure the needful economy in the liberation of the gas. A further advantage in the speedy adjustment to alterations in pressure is that there will be less expenditure of energy in the performance of ordinary movements, inasmuch as the Fish can readily find a plane of least effort; otherwise it would have to counteract a too feeble, or an increased specific gravity, by additional muscular effort. In the light of these considerations, but with the qualification which the absence of direct experimental evidence necessitates, we conclude that the Weberian mechanism not only confers on all Fishes that possess it an exceptional capacity for freedom of locomotion in the vertical direction, but also entails the contingent advantage that all movements will be effected with the maximum economy of muscular effort and tissue metabolism.

With regard to those Physostomi which have no Weberian mechanism, the evidence as to their ability to make use of the ductus pneumaticus as a means of pressure adjustment is very conflicting, and, moreover, it is not even certain that in all cases the duct is in free communication with the exterior. The frequent presence of retia mirabilia would also suggest that gaseous secretion and absorption are important factors in pressure adjustment. In the light of such contradictory evidence, no satisfactory conclusion is, at present, possible, but two alternative suggestions may be made. (*a*.) If the ductus pneumaticus cannot, from any cause, be used for pressure adjustment, gaseous secretion and absorption must be the only methods employed,

and, so far as the point is concerned, these Fishes must resemble the typical Physoclisti. (*b.*) On the other hand, even if it be admitted that some Physostomi, without the Weberian mechanism, can liberate gas through the ductus pneumaticus, it is nevertheless not difficult to see how it may be that the process is of little use to them for pressure adjustment. The completeness of the control exercised over the liberation of the necessary amount of gas will largely depend on the perfection of the reflex mechanism employed in the process, and in all the Fishes now under consideration the necessary afferent impulses must be initiated in the peripheral nervous system by the diffused pressure exerted by a distended air-bladder on the surrounding organs, instead of in a particular afferent nerve by a stimulus applied to a localised sensory epithelium through the Weberian mechanism, as is the case with the Ostariophyseæ. The indefinite character of the stimulus in the former would certainly militate against any delicacy in the responsive process of pressure adjustment. The more perfect afferent mechanism of the Ostariophyseæ conditions a more effective control over the function of the pneumatic duct, and a greater capacity for regulating the processes involved in pressure adjustment, and, as we have suggested, this is the great advantage which the Weberian mechanism confers upon all Fishes that possess it.

Certain structural adjuncts in connexion with the air-bladder of the Siluridæ may also be considered from a physiological point of view. These are, (1) the lateral cutaneous areas; (2) the "elastic-spring" apparatus of Müller; (3) the extrinsic muscles of the Pimelodinæ; and (4), the distinctive features of the air-bladder and Weberian mechanism in the Siluridæ as compared with other Ostariophyseæ.

1. The lateral cutaneous areas probably enable variations in the size of the anterior chamber of the air-bladder, the result of pressure variations, more promptly to modify the volume and therefore the specific gravity of the Fish, and consequently ensure a corresponding increase in the delicacy of the responsive processes involved in pressure adjustment.

2. Müller held the opinion that the "elastic-spring" apparatus is a mechanism for the condensation and rarefaction of the gases in the air-bladder. We cannot agree with Müller that the elastic springs can have any share in dilating the air-bladder or rarefying the gases which it contains, and it is doubtful if the apparatus can possibly give the Fish any power of directly compressing the bladder except under certain conditions, viz., when the anterior chamber becomes distended through the diminution of pressure which occurs during ascent in the water, coincidently with the forward or outward movements of the two springs as the result of the voluntary reflex con-

traction of their protractor muscles. We do not think with Müller that condensation is of use in facilitating descent; for a Fish in approximate equilibrium the slightest action of the ordinary locomotor organs is quite sufficient to produce either ascent or descent, and the existence of an elaborate mechanism for varying the internal capacity of the air-bladder and the volume of the enclosed gases with this object is altogether unnecessary. Sorensen's view that the mechanism is related to the production of voluntary sounds by the forcible expulsion of air through the pneumatic duct does not seem to us well founded, first, because the "elastic springs" are only able to forcibly compress the air-bladder during ascent, and, secondly, because sounds could only be produced in that way at the expense of a considerable disturbance of the normal equilibrium of the Fish in the water and of its locomotor activity. Two views may be taken as to the precise mode in which this singular mechanism is of practical utility: (1) the compression of the air-bladder may assist the action of the ductus pneumaticus in producing a more rapid ejection of gas during ascent; or (2) by condensation alone may counteract the effects of a too low specific gravity, and, at the same time, economise the contained gases. The latter alternative, in our opinion, is the more probable one.

3. The extrinsic muscles (compressor muscles) of the Pimelodinæ in all probability have a function similar to that of the "elastic-spring" apparatus. The function of the tensor tripodis muscle is probably to limit the violent excursions of the tripus, which otherwise would certainly take place when the bladder is forcibly compressed by the contraction of the compressor muscles.

4. The conclusion suggested by a comparison of the anatomical relations of the air-bladder and its associated skeletal structures is—that, physiologically considered, the most important distinctive features of the Weberian mechanism in the Siluridæ as compared with other Ostariophyseæ are mainly related to the air-bladder, which in the former attains its maximum degree of specialisation and delicacy as an organ adapted for the registration of varying hydrostatic pressures.

The Condition of the Air-bladder in the Siluridæ Abnormales.

The most noteworthy features in the structure of the air-bladder in the various genera of Siluridæ abnormales are: the absence of lateral chambers; the partial or complete constriction of the anterior chamber into two diminutive laterally situated air-sacs, which may lose all connexion not only with each other, but also with the œsophagus; and the occasional atrophy of the fibres by which the lateral walls of the bladder are normally connected with the tripodes.

Indications of retrogressive changes are not wanting in the auditory organ. In some, at least, of the Siluridæ abnormales the sinus endolymphaticus has completely atrophied, although the cavum sinus imparis and atrial cavities remain and retain their normal relations to one another and to the scaphia. The Weberian ossicles, on the other hand, are almost invariably complete. The few signs of degeneration which they exhibit relate to the straightness of the posterior processes of the tripodes, the suppression of the ascending and condylar processes of the scaphia, and, in a few instances, the absence of intercalaria.

Taking into consideration the retrograde changes both in the air-bladder and Weberian mechanism, it becomes almost impossible to believe that any hydrostatic function can be assigned to these structures, or that they do otherwise than present various states of modification towards the condition of vestigial and functionless organs, and this conclusion seems to us equally inevitable whatever may have been their original function.

Of the one hundred and sixteen genera mentioned in the British Museum Catalogue no fewer than twenty-five at least are referable to the Siluridæ abnormales. The causes that have led to the degeneracy of the air-bladder in so many forms are in many instances not difficult to trace, and, as in so many Physoclist Teleostei, the assumption of a purely ground habit of life is probably the most important one. Not a few of the genera of Siluridæ abnormales inhabit the comparatively shallow waters of rapidly flowing mountain streams and torrents, often being at a considerable altitude, and in general habit are not unlike our common English Loaches. Many are provided with an adhesive apparatus on the ventral surface of the body between the pectoral fins, so that they may be enabled to withstand the force of mountain torrents. Such Fishes when not in motion probably rest upon or attach themselves to the river bottom, and the uselessness and probable harmfulness of an air-bladder as a hydrostatic organ under such conditions is no doubt the cause of its degenerate and rudimentary condition. Various species of *Callichthys* are said to keep under plants in marshy swamps, to be able to burrow in the mud, in which they often become dried up, and even to be capable of migration upon land in search of water; similar habits characterise other forms.

The susceptibility of the air-bladder to change of habitat or habits on the part of its possessor is well shown by the variation that may be met with in the same genus. Two species of *Cryptopterus* (*C. micropus* and *C. hexaptera*) have rudimentary air-bladders, while all the remaining species of the genus which came under our notice have these organs unusually well developed. In two species of *Pimelodus* also (*P. pulcher* and *P. sapo*) the air-bladder is not only

rudimentary but lacks even a trace of the compressor and tensor tripodis muscles which are so characteristic of the normal Pimelodinæ. Probably in such instances the degeneration of the air-bladder is due to the assumption of a ground habit.

The invariable persistence of the Weberian ossicles in an almost structurally complete but functionless condition may be explained by the absence of any potent cause calculated to bring about their total suppression.

The uniform retention of the anterior chamber in these Siluroids while the lateral compartments have almost invariably disappeared, in place of the entire suppression of the air-bladder which occurs in most other Teleostei whenever that organ from similar causes has become useless to its possessor, is due to its connection with the persistent Weberian ossicles.

The encapsulation of the air-bladder by bone is difficult to explain satisfactorily, but two alternative suggestions may be made. (1.) Encapsulation varies greatly in extent as well as in the precise methods by which it has been brought about, but very often appears to bear some relation to the structural completeness of the diminutive air-bladder and the retention of its apparently functional connexion with the Weberian ossicles. Where the air-bladder retains much of its structural integrity encapsulation is always more complete than when the contrary is the case, and may then be due to the necessity of preventing any distension of the reduced and useless organ by varying external pressures from imparting disturbing and useless stimuli to the internal ear. On the other hand, encapsulation is always less complete when structural lesions are too obvious to admit of any possibility of pressure variations affecting the Weberian ossicles, and the fact that it exists at all in such cases may be explained by the supposition that reduction in the size of the only portion of the air-bladder that persists, that is, the anterior chamber, has been accompanied by a corresponding contraction and curvature of the modified transverse processes which normally invest, and are closely moulded to, its anterior and dorsal surfaces. (2.) Encapsulation may be due in part to the tendency of the transverse processes to contract round and envelope an atrophying air-bladder, and in part also to an unchecked development of that tendency to ossification of the walls of the air-bladder, or of the investing connective tissue, which to a restricted extent is so characteristic a feature even in the normal Siluroids.

Of the remaining families of the Ostariophyseæ, the Cyprinidæ exhibit a substantially similar and parallel series of modifications in the condition of the air-bladder, which, it can scarcely be doubted, are also correlated with the assumption of a grovelling and purely "ground" habit of life, and, as in certain Siluridæ abnormales, the

invariable completeness of the encapsulation of the reduced air-bladder by bone in the former may be associated with the fact that both the bladder and the Weberian mechanism otherwise retain their normal structural integrity.

Geographical Distribution of the Ostariophyseæ.

All the Ostariophyseæ are fresh-water forms, except a few Siluroids which have become accustomed to a marine habitat. Of the known 2180 (approximate) fresh-water Teleostei, there are only about 600 in which the Weberian apparatus is absent. Broadly speaking, it may be stated that the total number of species of Ostariophyseæ is nearly five times as great as all the other species of fresh-water Physostomi; nearly five times greater than the species of fresh-water Physoclisti; and about three times the number of the species of Physostomi and Physoclisti combined. With the exception of the Gymnotidæ and Gymnarchidæ, the families of the Ostariophyseæ are, so far as species are concerned, from two to six times as large as the best represented families of the remaining Physostomi or the Physoclisti; and the families of the Cyprinidæ and Siluridæ are by far the richest, both in species and genera, the former including one-third (724), and the latter about one-fourth (572), of all the known fresh-water species. This predominance characterises all the great zoo-geographical regions about which we have any information, with the exception of North America, where other fresh-water Fishes slightly outnumber the Ostariophyseæ. In the Indian and Neotropical regions, where fresh-water Fishes attain their maximum degree of specific development, the Ostariophyseæ outnumber all the remaining species in those districts in the proportions of 5·5 and 4 to 1 respectively. The great rivals to the Ostariophyseæ among fresh-water Fishes are the Salmonidæ and Cyprinodontidæ, but, owing to a difference of habit, or of geographical distribution, a considerable number of their species do not come into direct competition with the former.

Hence, it may be concluded that the possession of a Weberian mechanism is specially characteristic of the dominant families of fresh-water Teleostei, that is, of those families which combine to the greatest extent numerical strength in individuals, richness in specific differentiation, and wideness of geographical distribution.

Two other possible conclusions are also suggested by these facts: (1) that the possession of a Weberian mechanism is directly related to certain peculiarities of a fresh-water habitat, and (2) that the close association between the presence of this mechanism and the marked ascendency of the Ostariophyseæ over all other families of fresh-water Teleostei points to the possibility that the relation is one of cause and effect. Both conclusions, in our opinion, are highly probable, and the

demonstration of the first would almost necessarily involve the truth of the second, but positive proof of either is extremely difficult. To prove the correctness of the first, it must be shown that there are certain conditions involved in a fresh-water habitat which render the possession of a Weberian mechanism of special value to fresh-water Fishes. If, as we have suggested, the mechanism confers upon all Fishes which possess it an exceptional capacity for locomotion in all directions, with a minimum of muscular effort, it seems reasonable to anticipate that such advantages are of greater importance to fresh-water species than to their marine congeners.

The poverty of fresh-water faunas, as compared with marine, and the entire absence of certain groups of organisms which are abundant in the sea, are among the most obvious facts in the geographical distribution of animals. Of the special external conditions which have combined to produce these results, the most obvious, and perhaps the most important, are, (*a*) existence in a medium which, omitting lakes, is always in motion in a definite direction; and (*b*) a more precarious and fluctuating food supply, due to climatic severity, alternations of seasons (such as winter and summer, dry and rainy seasons), and to the isolation and comparative smallness of fresh-water areas. On the other hand, the relation of Fishes to other forms of fresh-water life is in many respects unique. No other groups of equivalent taxonomic value approach Fishes in richness of specific differentiation or individual size, and it is equally clear that the predominancy of Fishes is mainly due to the numerical strength of the Ostariophyseæ, both in individuals and in genera and species. It is, therefore, not unreasonable to infer that, for some reason, the special conditions of a fresh-water existence are less adverse to Fishes than to any group of organisms, and, further, that the Ostariophyseæ apparently possess an altogether exceptional capacity for adapting themselves to conditions which, in almost all other cases, are inimical, both to individual and specific development. Can it be shown that there is any definite relation between any of the conditions of a fresh-water life and the advantages derivable from the possession of a Weberian mechanism?

Of the special conditions of a fresh-water habitat, we lay most stress on the precarious and fluctuating character of the food supply, and a comparison of the relative positions of fresh-water and marine Fishes from this point of view suggests a possible answer to the question. The food supply of marine Fishes is less precarious and less liable to quantitative fluctuations than in the case of fresh-water species, and, moreover, local scarcity of food may be met by migration to areas where, for the time being, food is more abundant. With fresh-water Fishes the converse holds good, and in their case the restricted extent and comparative isolation of fresh-water areas are,

in general, an insuperable obstacle to migration as a means of remedying local scarcity. The poverty of most other forms of fresh-water life absolutely conditions the existence of a relatively larger number of herbivorous or omnivorous Fishes in fresh waters than in the sea, where the abundance and variety of other animal organisms are so much greater, and this necessarily involves the existence of a piscine fauna, which, from the nature of the food supply, is to a large extent peculiarly liable to the exigencies of a precarious and inconstant food supply. It can also be shown that marine Fishes are more voracious than fresh-water, and that while the latter may survive total abstinence from food for weeks or months, the former succumb within a few days. The majority of the Ostariophyseæ appear to be herbivorous or omnivorous, while the capacity of many of them for accumulating reserve food material, at the expense of which they live during the seasons of relative scarcity, has often been remarked.

Not only do marine Fishes differ from the majority of fresh-water species in the greater constancy and abundance of their food supply, but they also differ from the latter in their method of pressure adjustment. Relying, as the former do, upon the relatively slow processes of gaseous secretion and absorption, any departure from the plane in which, for the time being, they are in equilibrium must involve a decrease or increase of specific gravity to an extent proportional to the amount of pressure variation. Hence, in ordinary rapid locomotor movements, involving more or less extensive changes of level and pressure, there must be an increase of muscular exertion, which will necessarily be greater in proportion as the Fish departs from its normal plane of equilibrium. In the great majority of fresh-water Fishes, that is to say, in the Ostariophyseæ, pressure adjustment is more accurate and rapid, so that in all variations of level and pressure, whether rapidly or slowly brought about, but more especially under conditions of diminished pressure, the Fish always retains a normal plane of least effort, with the result that its locomotor movements will be accompanied by a minimum expenditure of muscular effort. It may therefore be inferred that, as a general rule, marine Fishes are exposed to greater demands upon their muscular energy than is the case with fresh-water species—a difference which must always be associated with the more favourable nutritive conditions under which the former exist, as compared with the more precarious food supply of the latter—while, at the same time, it affords a reasonable explanation of the relative capacities of marine and fresh-water Fishes for enduring prolonged abstinence from food.

If we do not overrate the importance of these considerations, it is obvious that, in view of the precarious and fluctuating character of

their food supply, economy in the expenditure of muscular energy must be of primary importance to the majority of fresh-water Fishes, and more particularly to those which, wholly or in part, derive their food from vegetable sources. Hence, the possession of any mechanism which will not only remove all restrictions to motion in the vertical direction, and thereby enlarge the area within which food may be obtained, but, at the same time, will also enable those Fishes to execute all locomotor movements with the least possible expenditure of muscular effort, must prove to be a great physiological advantage to them, inasmuch as economy of muscular effort implies diminished tissue metabolism, and, consequently, indirectly but effectually aids the accumulation of the nutritive reserve, at the expense of which the Fish subsists during the lengthened periods when fresh food is relatively scarce. It may be that this is precisely the advantage which the possession of a Weberian mechanism enables all Ostariophyseæ to realise—an advantage which, as we venture to suggest, is one of the main causes of their marked ascendency over all other fresh-water species in which this mechanism is wanting, and with which they come into direct competition.

As no other attempt has been made to associate the evolution of the Weberian mechanism with any special peculiarities of external environment, we would suggest the following tentative conclusions:—

1. The special feature of a fresh-water habitat that has conditioned the development of the Weberian mechanism in the Ostariophyseæ is the occurrence of seasonal or periodic quantitative variations in the food supply, variations to which the Ostariophyseæ, from their herbivorous or omnivorous habits, are specially liable.

2. In view of such unfavourable nutritive conditions, the special advantage which is conferred upon the Ostariophyseæ by the possession of the Weberian mechanism is a capacity for executing locomotor movements in any plane, with an almost irreducible minimum of muscular effort and tissue metabolism.

3. If a variable and inconstant food supply is to be regarded as one of the inevitable conditions of a fresh-water existence, and necessitates strict economy in the expenditure of muscular energy, any mechanism which secures this result must be of unquestionable importance to the species, and hence it may be that the Ostariophyseæ owe their dominant position among fresh-water Fishes to the possession of the Weberian mechanism.

4. The evolution of the Weberian mechanism has not only conditioned the predominancy of the Ostariophyseæ, but, indirectly, has favoured the existence in fresh water of a large number of purely carnivorous Fishes, which depend on the former for their food, and therefore may also be regarded as one of the primary causes of the

anomalous abundance and diversity of fresh-water piscine life, as compared with the remarkable poverty of all other groups of fresh-water organisms.

Concluding Remarks.

The varied structural modifications met with in the air-bladder cf the Siluridæ are not surprising, in view of the exceptionally diversified conditions under which the different species and genera live. The physical conditions under which many Siluridæ are capable of living are almost as varied as their geographical distribution or climatic range.

Darwin has pointed out, in referring to the conditions favourable to variation in animals and plants, that it is common, widely diffused, and widely ranging species that vary most, and that this might be expected from the diverse physical conditions to which they would be exposed, as well as from differences in the nature and quality of their living competitors in different regions. Further, he alludes to the fact that an organ developed in an extraordinary manner implies that it is of high functional importance to the species, and that it may also be concluded that the organ has undergone a great amount of variation since it first came into existence. It is clear that the Siluridæ furnish an admirable illustration of the truth of these remarks.

Nor is it difficult to see how it is that the Weberian apparatus and air-bladder are more specialised in the Siluridæ than in other Ostariophyseæ. The only rivals to the Siluridæ in the extent of their geographical distribution are the Cyprinidæ, for the remaining families have but a comparatively restricted range. But, extensive as is their geographical distribution, the great majority of the Cyprinidæ appear to exist under fairly uniform conditions, or, at all events, exhibit nothing like the diversity of habitat and habits that is so characteristic of the Siluridæ, and hence it is that, so far as the structure of the air-bladder and Weberian mechanism is known in the former family, it presents but little variation in the direction of increased specialisation, although in a few genera the effects of degeneration are sufficiently obvious.